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ON A THEOREM OF VON NEUMANN

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J. von Neumann pointed out in a recent talk at Harvard the need for an elementary proof of the following theorem, which was originally proved by him using the Brouwer fixed-point theorem.[1, 2] The present note supplies such a proof.

THEOREM. *Let a_{ij} and b_{ij} be two rectangular matrices ($i = 1, \ldots, n$; $j = 1, \ldots, m$) such that $a_{ij} > 0$ for all i, j. Then there exists a unique λ and vectors $x = (x_1, \ldots, x_m)$, $y = (y_1, \ldots, y_n)$ subject to $x_j \geqq 0$, $y_i \geqq 0$, $\Sigma_1^m x_j = 1$ and $\Sigma_1^n y_i = 1$, such that*

$$\lambda \sum_{j=1}^{m} a_{ij}x_j \geqq \sum_{j=1}^{m} b_{ij}x_j, \; i = 1, \ldots, n, \tag{1}$$

$$\lambda \sum_{i=1}^{n} a_{ij}y_i \leqq \sum_{i=1}^{n} b_{ij}y_i, \; j = 1, \ldots, m. \tag{2}$$

Let X be the set of m-dimensional vectors $x = (x_1, \ldots, x_m)$ such that $x_j \geqq 0$, $j = 1, \ldots, m$ and $\Sigma_1^m x_j = 1$, and let Y be the corresponding set of n-dimensional vectors. Let (2′) be the inequalities (2) with λ replaced by μ. It is evident that λ and x in X satisfying (1) exist, and that μ and y in Y satisfying (2′) exist. Moreover (1) and (2′) yield

$$\mu \sum_{i}\sum_{j} a_{ij}y_i x_j \leqq \sum_{i}\sum_{j} b_{ij}y_i x_j \leqq \lambda \sum_{i}\sum_{j} a_{ij}y_i x_j \tag{3}$$

In particular, $\mu \leqq \lambda$, so that the values of λ which can be used in (1) are bounded below, and since X is compact, the greatest lower bound λ_0 can be used in (1) for a certain vector x^0. Similarly the least upper bound μ_0 can be used in (2′) for a certain vector y^0. And $\mu_0 \leqq \lambda_0$.

The theorem deals with those λ of (1) which are also μ of (2′). Clearly the only λ having this property is $\lambda = \lambda_0$, and even this will not do if $\mu_0 < \lambda_0$. Hence we must prove that $\mu_0 = \lambda_0$.

The proof of the theorem is an induction on $m + n$. If $m + n = 2$, the theorem is trivial. In the general case, if equality occurs in (1) for all $i = 1, \ldots, n$ when $\lambda = \lambda_0$, $x = x^0$ and also in (2′) for all $j = 1, \ldots, m$ when $\mu = \mu_0$, $y = y^0$, then equality occurs in (3), so that $\mu_0 = \lambda_0$ and the theorem is established. It remains only to consider the case when strict in equality holds at least once. We may suppose therefore that

$$\lambda_0 \sum_j a_{ij} x_j^0 = \sum_j b_{ij} x_j^0, \; i = 1, \ldots, n_1,$$
$$\lambda_0 \sum_j a_{ij} x_j^0 > \sum_j b_{ij} x_j^0, \; i = n_1 + 1, \ldots, n. \tag{4}$$

Let λ_1 and μ_1 be the extreme values of λ and μ in (1) and (2′) for the reduced matrices ($i = 1, \ldots, n_1$; $j = 1, \ldots, m$). Then

$$\lambda_1 \leqq \lambda_0, \; \mu_1 \leqq \mu_0. \tag{5}$$

For, every λ and $x = (x_1, \ldots, x_m)$ satisfying (1) for $i = 1, \ldots, n$ also satisfies (1) for the reduced set $i = 1, \ldots, n_1$. And every μ and $y = (y_1, \ldots, y_{n_1})$ satisfying the reduced (2′) (with n replaced by n_1 in the sums) also satisfies the original (2′) if y is extended to $y = (y_1, \ldots, y_{n_1}, 0, \ldots, 0)$. We assert that in fact $\lambda_1 = \lambda_0$. Suppose, on the contrary, that $\lambda_1 < \lambda_0$, and that λ_1 is assumed at $x = x'$, i.e., that

$$\lambda_1 \sum_j a_{ij} x_j' \geqq \sum_j b_{ij} x_j', \; i = 1, \ldots, n_1. \tag{6}$$

Then if $x = \alpha x^0 + (1 - \alpha)x'$, where $0 < \alpha < 1$ (note that $x \epsilon X$), we have from (4) and (6) that

$$\lambda_0 \sum_j a_{ij} x_j > \sum_j b_{ij} x_j, \; i = 1, \ldots, n_1, \tag{7}$$

and it follows from (4) and the continuity of the expressions involved that (7) remains true for $i = n_1 + 1, \ldots, n$ if α is small enough. Hence λ_0 is not the extreme value for (1), a contradiction. Thus $\lambda_0 = \lambda_1$. But $\lambda_1 = \mu_1$ by the inductive hypothesis, $\lambda_1 \leqq \mu_0$ by (5) and $\mu_0 \leqq \lambda_0$ from (3). Therefore, $\mu_0 = \lambda_0$ and the theorem has been proved.

If $\mu = \mu_0 = \lambda_0 = \lambda$, $x = x^0$, $y = y^0$, then (3) becomes an equality. Therefore, if strict inequality holds in (1) at $i = i_0$ then $y_{i_0}^0 = 0$, and similarly if strict inequality holds in (2′). If the matrices are square and b_{ij} is the unit matrix, it is evident from (1) that $\lambda_0 (= \mu_0) > 0$, so that (2′) implies that $y_i^0 > 0$ and (1) is composed of equalities. But then $x_j^0 > 0$ and (2′) is composed of equalities. Thus we deduced as a corollary the existence of a positive proper value and the associated positive proper vectors for a positive matrix and its transpose.

For the application of the theorem to the theory of production, see reference 1. The special case where all $a_{ij} = 1$ is important in the theory

of games. For this see reference 3, pp. 154–155, where another proof of this special case is also referred to.

[1] von Neumann, J., "Über ein ökonomisches Gleichungssystem, etc.," *Ergebnisse eines Mathematischen Kolloquiums*, **8**, 73–83 (1937).

[2] Kakutani, S., "A Generalization of Brouwer's Fixed Point Theorem," *Duke Math. Jour.*, **8**, 457–459 (1941).

[3] von Neumann, J., and Morgenstern, O., "Theory of Games and Economic Behavior," Princeton University Press (1944).

ON BLOCKS OF CHARACTERS OF GROUPS OF FINITE ORDER, II

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1. The first part of this investigation appeared in these PROCEEDINGS, June, 1946, p. 182.[1] In this note, we shall apply our results to a study of the (generalized) decomposition numbers[2] of a group G of finite order g and of the arithmetic in the group ring Γ of G.

Let again p be a fixed rational prime number. Select a full system Π of elements $\pi_0 = 1, \pi_1, \pi_2, \pi_3, \ldots$ of orders $1, p, p^2, \ldots$ such that every element of an order p^α of G is conjugate in G to exactly one element π_i of Π. Denote by N_i the centralizer of π_i in G. A full system Σ of elements of G representing the different classes of conjugate elements can be obtained in the following manner: Let $\sigma_1^{(i)}, \sigma_2^{(i)}, \ldots$ represent the different p-regular classes of conjugate elements of N_i. Then Σ consists of the elements $\pi_i\sigma_1^{(i)}, \pi_i\sigma_2^{(i)}, \ldots$ for $i = 0, 1, 2, \ldots$.

2.[3] If $\zeta_1, \zeta_2, \ldots, \zeta_k$ are the ordinary irreducible characters of G, and if $\varphi_1^i, \varphi_2^i, \ldots$ are the modular irreducible characters of N_i, then for every p-regular element σ of N_i, we have a formula

$$\zeta_\mu(\pi_i\sigma) = \sum_\nu d_{\mu\nu}^i \varphi_\nu^i(\sigma) \qquad (1)$$

where the $d_{\mu\nu}^i$ are algebraic integers, the *decomposition numbers*, which are independent of σ. This formula yields a representation of the matrix $\mathbf{Z}$ of the ordinary characters of G as a product of two square matrices D and Φ

$$\mathbf{Z} = D\Phi. \qquad (2)$$

We have to set $\sigma = \sigma_j^{(i)}$, $\mathbf{Z} = (\zeta_\mu(\pi_i\sigma_j^{(i)}))$, where μ is the row index while every column corresponds to an element $\sigma_j^{(i)}$, $i = 0, 1, 2, \ldots$; $j = 1, 2, \ldots, k_i$, where k_i is the number of p-regular classes of N_i. Similarly, in D =

$(d^i_{\mu\nu})$, the rows correspond to the characters ζ_μ and the columns to the modular characters φ^i_ν, of the different N_i. Finally, if the rows and columns are arranged suitably,

$$\Phi = \begin{pmatrix} (\varphi^0_\nu(\sigma^{(0)}_j)) & 0 & \dots \\ 0 & (\varphi^1_\nu(\sigma^{(1)}_j)) & \dots \\ \dots & \dots & \dots \end{pmatrix} \tag{3}$$

where, in each partial matrix $(\varphi^i_\nu(\sigma^{(i)}_j))$ in the main diagonal, the row index is ν and the column index is j.

The degree of all three matrices in (2) is equal to the number k of conjugate classes of G,

$$k = k_0 + k_1 + \dots,.$$

The square of the determinant of D is a power of p while the determinant of Φ is relatively prime to p. The formulae (1) show that in order to know the ordinary characters of G, it is sufficient to know the modular characters φ^i_ν of all the N_i including $N_0 = G$, and the decomposition numbers $d^i_{\mu\nu}$. Actually, the product of the column (i, ν) of D with the conjugate complex of the column (i', ν') is 0 for $i \neq i'$ and the Cartan invariant $c^i_{\nu,\nu'}$ of N_i for $i = i'$. While this $c^i_{\nu,\nu'}$, can be expressed in terms of the φ^i_ν, this does not enable us to express the decomposition numbers in terms of the φ^i_ν.

We shall say that for fixed i the elements $\pi_i\sigma^{(i)}_j$ of G belong to the ith *section*.

3. In the notation of I, theorem 1, we take H as the group generated by σ_i, and $M = \mathfrak{C}(H) = N_i$. The following result can be proved (with considerable difficulty):

THEOREM 1: *If the modular character φ^i_ν of N_i belongs to a block $\tilde{B}_\sigma$ of N_i, then $d^i_{\mu\nu}$ can be different from 0 only for ordinary characters of G which belong to the block B_τ of G determined by $\tilde{B}_\sigma$.*

This implies that in each column of D we have zero except in the rows corresponding to the ζ_μ belonging to one block B_τ of G. It follows that, if the rows and columns of D are taken in a suitable order, D breaks up completely into t matrices $T_1, T_2, \dots, T_t$, each T_τ corresponding to one block B_τ, $(\tau = 1, 2, \dots, t)$. Since $\det D \neq 0$, each T_τ must necessarily be a square matrix, of degree x_τ, where x_τ is the number of ordinary characters in B_τ. The arrangement of the columns of D here will in general not be the same as that used in (2).

Originally, only the ordinary characters ζ_μ of G and the modular characters φ^0_ν, of G itself were distributed into blocks B_τ. It is now natural to count φ^i_ν, $i \geqq 0$, as a character of B_τ, if φ^i_ν belongs to a block $\tilde{B}_\sigma$ of N_i which determines B_τ in the sense of I. Then B_τ consists of x_τ ordinary characters ζ_μ and x_τ modular characters φ^i_ν. In our notation, y_τ of these characters have the upper index $i = 0$. These are the modular characters of G, the other φ^i_ν are the modular characters of the groups N_i.

As a corollary to theorem 1, we have the following refinement of some of the orthogonality relations for group characters.

THEOREM 2: *If the elements ρ and σ of G belong to different sections of G, then*

$$\sum_{\mu}{}' \zeta_\mu(\rho)\zeta_\mu(\sigma) = 0$$

when in the sum ζ_μ ranges over all the characters of G belonging to a fixed block B_τ.[4]

4. We state without proof the following results which are connected with theorem 1.

THEOREM 3: *Let B_τ be a block of G, and D_τ its defect group. If no element of D_τ is conjugate to π_i, then $\zeta_\mu(\rho) = 0$ for all characters ζ_μ of B_τ and all elements of the section of π_i.*[5]

THEOREM 4: *If B_τ is a block of defect d_τ with the defect group D_τ, there exist blocks $\tilde{B}_\sigma$ of defect d_τ of N_i which determine B_τ, if and only if π_i is conjugate in G to an invariant element of D_τ. If π_i is conjugate to an invariant element of D_τ, we can choose the block $\tilde{B}_\sigma$ of defect d_τ of N_i in such a manner that it determines the block B_τ of G, and that for every ζ_μ in B_τ there exists a φ_ν^i in $\tilde{B}_\sigma$ such that $d_{\mu\nu}^i \not\equiv 0$.*

Let p^a be the exact exponent to which p divides g,

$$g = p^a g', \quad (p, g') = 1$$

If $\mathfrak{p}_0$ is a prime ideal divisor of p in the field of characters, and if the degree z_μ of ζ_μ contains p to the exact exponent $a - d_\tau + \epsilon$, $(\epsilon \geqq 0)$, we may even state in theorem 4 that for a suitable φ_ν^i in B_τ we have

$$d_{\mu\nu}^i \not\equiv 0 \pmod{p^\epsilon \mathfrak{p}_0}. \tag{4}$$

THEOREM 5: *If the block $\tilde{B}_\sigma$ of N_i determines the block B_τ of G, the defect of $\tilde{B}_\sigma$ is at most equal to l, where p^l is the order of a maximal p-subgroup of N_i which is conjugate in G to a subgroup of the defect group D_τ of B_τ. If the degree z_μ of the character ζ_μ of B_τ is not divisible by p^{a-d+1} where d is the defect of B_τ, there exists a character φ_ν^i of N_i which belongs to a block of N_i of defect l and for which $d_{\mu\nu}^i$ is not divisible by $\mathfrak{p}_0$.*

THEOREM 6: *If p^α is the maximal order of elements of the defect group D_τ of B_τ, then for all ζ_μ in B_τ, the numbers $d_{\mu\nu}^i$ belong to the field of the p^α-th roots of unity. The characters ζ_μ of B_τ belong to the field of the $(p^\alpha g')$-th roots of unity.*

THEOREM 7: *If $p \neq 2$, and if B_τ contains y_τ modular characters of G, then at least y_τ of the ordinary characters ζ_μ of B_τ are p-rational, that is, they lie in the field of the g'-th roots of unity, $(g', p) = 1$.*

In fairly general cases, the exact number of p-rational characters in B_τ is equal to y_τ.

For $p = 2$, a result similar to theorem[7] can be obtained which is more complicated, and shall not be stated here.

5. The previous results make it possible to prove the following theorem:

THEOREM 8: *A block B of defect d contains at most* $p^{d(d+1)/2}$ *ordinary characters.*

It is probable that the bound $p^{d(d+1)/2}$ here can be replaced by p^d, but I have been able to prove this stronger result only for $d = 0, 1, 2$.

Theorem 8 implies that if the order g of a group is divisible by the prime number p to the exact exponent a, and if G contains q classes of conjugate elements whose order is prime to p but whose normalizer has an order divisible by p^a, then at most $qp^{a(a+1)/2}$ of the degrees of ordinary irreducible representations of G are relatively prime to p.

6. As in I, let K be an algebraic number field in which all the simple constituents of the semisimple algebra Γ split completely. Denote by $\mathfrak{p}$ a fixed prime ideal divisor of p in K. The ideal $(\mathfrak{p})$ generated by $\mathfrak{p}$ in the ring of integers J of Γ can be represented as a direct intersection[6]

$$(\mathfrak{p}) = \mathfrak{M}_1 \cap \mathfrak{M}_2 \cap \ldots \cap \mathfrak{M}_t$$

of ideals of J, such that no $\mathfrak{M}_\tau$ possesses a proper representation as direct intersection. There exists a $(1 - 1)$ correspondence between these "block components" $\mathfrak{M}_\tau$ of $(\mathfrak{p})$ and the blocks B_τ of characters of G (for p). In particular, the number y_τ of modular characters of G is equal to the number of prime ideals $\mathfrak{P}$ of J dividing $(\mathfrak{p})$. Now, theorem 8 implies

THEOREM 9: *No block component of* $(\mathfrak{p})$ *in J is divisible by more than* $p^{a(a+1)/2}$ *prime ideals of J where* p^a *denotes again the highest power of p dividing g.*

The y_τ^2 coefficients of the Cartan matrix C_τ of the block B_τ describe, to a certain extent, the mutual relationship between the y_τ prime ideal divisors $\mathfrak{P}$ of $\mathfrak{M}_\tau$. They represent interesting arithmetical invariants. Here, C_τ is a symmetric matrix with integral rational coefficients. We can form the corresponding quadratic form Q. Now our results yield

THEOREM 10: *To given p and given defect d, there exist only a finite number of classes of quadratic forms to which the Cartan form Q of a block of defect d can belong (for an arbitrary group G of finite order).*

We also quote the following results which can be proved directly without great difficulty.

THEOREM 11: *If the defect of the block* B_τ *is positive, the Cartan form Q does not represent the number 1. More generally, Q does not represent (integrally) a form of determinant 1.*

If B_τ has the defect 0, then C_τ is of degree 1, and Q is the quadratic form x^2.

7. It may be remarked that blocks of defect 1 can now be discussed rather completely. The results obtained earlier for the characters of groups

of an order $g = pg'$, $(p, g') = 1$ appear as special cases of properties of characters of blocks of defects 0 and 1.[7]

Finally, it may be mentioned as a conjecture that it appears probable that for a given p and d, only a finite number of matrices exist which can occur as Cartan matrices C_τ of blocks of defect d.

[1] The first part will be quoted as I.

[2] Cf. Brauer, R., *Ann. Math.*, **42**, 926–935 (1941).

[3] For the results quoted in this section, cf. the paper mentioned in [2].

[4] In the case that ρ belongs to the section of the 1-element, this result has already been obtained in Brauer, R., and Nesbitt, C., *University of Toronto Studies, Math. Ser.*, No. 4, theorem VIII (1937).

[5] This generalizes a result obtained in Brauer, R., and Nesbitt, C., *Ann. Math.* **42**, 556–590 (1941) for blocks of defect 0.

[6] Cf. Brauer, R., these PROCEEDINGS, **30**, 109–114 (1944), in particular, equation (2).

[7] Cf. Brauer, R., these PROCEEDINGS, **25**, 290–295 (1939), and *Ann. Math.* **42**, 936–958 (1941).

I take this occasion to mention the following corrections in the first of these papers: In theorem III, the assumption should read $n < (2p + 7)/3$. The left side of equation (4) should read $r_\rho t_\mu + r_\mu t_\rho$. For the results of the last paragraph of section 3, it is necessary to assume that a suitable splitting field is used.

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*EFFECTS OF EXPOSURE TO ULTRA-VIOLET LIGHT ON HUMAN DARK ADAPTATION**

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Previously it has been shown that the course of dark adaptation of the eye of the baby chick can be altered by addition of ultra-violet radiation between 290 and 365 mμ to the visible white light of a mercury vapor lamp during preëxposure.[1] Exposure to wave-lengths longer than 365 mμ results in uniform dark adaptation curves, all curves reaching the same final threshold level. The addition of ultra-violet below 365 mμ retards complete adaptation, raising the final threshold considerably above the normal. Extension of the ultra-violet range to about 355 mμ causes an increase of 0.3 log unit, to 315 mμ an increase of 0.6 log unit, and to 290 mμ an increase of 1.1 log units in the final threshold level.

In the baby chick, as in all newly born animals, the absorption by the ocular media is small, therefore a considerable penetration of ultra-violet to the retina is expected. For the human eye the ultra-violet transmission is a function of age,[2] depending mainly upon the transparency of the lens;[3] it is maximal in infancy and thereafter decreases so that in the adult eye

the lens transmission at 365 mμ is only 0.1 per cent.[4] In accordance with this fact one might assume *a priori* that wave-lengths shorter than 365 mμ can have practically no effect upon the retina. In subsequent tests it is demonstrated that addition of ultra-violet to the adapting light during preëxposure changes the course of human dark adaptation and raises the final level of adaptation, and thus decreases the sensitivity of the eye.

Light Exposure.—The observer must be fully light adapted before the course of dark adaptation can be studied. As light source, a 250-watt mercury vapor lamp (GE type H-5) is used. The lamp is mounted in a housing 50 cm. behind a finely ground round Pyrex plate (transmitting from 285 mμ up), 30 cm. in diameter, which acts as a diffusing screen. The observer views this evenly illuminated screen from a distance of 50 cm., securing uniform light exposure of a large retinal area. Between lamp and screen, filters of different transmissions can be inserted which provide for addition of smaller or larger portions of the ultra-violet part of the spectrum to the otherwise white exposure light. The filters used are: AO crown 1045, transmitting from 290 mμ up; ordinary plate glass, transmitting above 315 mμ; AO Cruxite 1794 transmitting above 355 mμ; and Corning 3389 (Noviol, shade A), which begins to transmit at about 410 mμ. All filters have practically the same transmission in the visible, therefore the color of the exposure light does not change. The brightness of the screen as measured with a Macbeth Illuminometer is 6250 millilamberts. To this illumination varying only in ultra-violet content the observer is exposed prior to test for a standard period of 10 minutes.

Measurements.—The course of dark adaptation is followed with the aid of a visual discriminometer,[5] an instrument of highest experimental rigidity, particularly in regard to fixation, retinal location of the test field, size of the field and control of threshold intensities of light. The instrument is calibrated by insertion of the illuminometer into one tube of the binocular head, after removal of the eyepiece. After completion of light exposure the observer views monocularly a red fixation point, representing the center of a square test field, subtending a visual angle of 12.5° on a side. With good fixation and the head securely on a chin rest, the test field is presented by means of a shutter for $^1/_{25}$ second, while by a neutral-tint wedge the operator of the instrument increases step by step the intensity of the field for each flash, until the critical point of first perception of the flash is reached. The time from cessation of light exposure and the wedge reading is recorded. This procedure is continued for 30 to 35 minutes, until there is no further increase in sensitivity at complete adaptation.

With exposure light free from ultra-violet (Noviol A in the light path) the ensuing dark adaptation curve is duplex, separating the process of adaptation into a cone and a rod component. The cone segment of the curve covers about 1.3 log units between the first reading, taken roughly at 1

minute, and the onset of the rod segment of the curve. The transition from cone to rod adaptation occurs after about 6.5 minutes. By adding to the exposure light ultra-violet down to 290 mμ by the insertion of crown glass into the light path instead of Noviol, the course of adaptation is modified. While the general level of the cone curve remains unchanged, it is extended up to 8 minutes, overshooting the previous onset of rod adaptation by $1^1/_2$ minutes. Rod adaptation then follows a course parallel to that obtained without the ultra-violet but on a higher intensity level, so

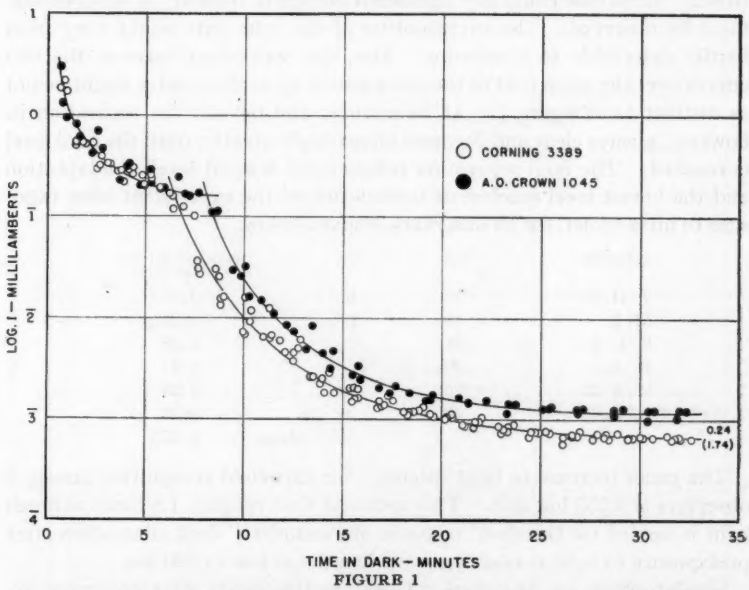

FIGURE 1

The course of dark adaptation of the human eye after preëxposure to light free from ultra-violet (Corning 3389, Noviol, shade A) in the light path (open circles) and light containing ultra-violet as low as 290 mμ (Crown in the light path), black circles. The ultra-violet produces a later onset of rod adaptation and raises the threshold levels for the rod segment.

that at complete adaptation the two curves are separated by 0.24 log unit which corresponds to an increase in threshold intensity by a factor of 1.74 for threshold recognition.

In figure 1 summarized data on one observer are presented. There are plotted 6 runs with Noviol and 3 runs with crown in the path of the exposure light. The observations extend over several days. A run with crown may follow a run with Noviol immediately. After crown a minimum time of 5 hours was allowed so that no previous ultra-violet effects would inter-

fere with a subsequent run. The data in figure 1 represent the prototype of the course of dark adaptation without and under the influence of ultra-violet in the exposure light. Altogether, measurements were taken on 6 observers which show in principle the same kind of phenomena. In each case a higher "final" threshold of the rod segment is found after preexposure to light filtered by crown only. The rise in "final" threshold varies between 0.21 and 0.29 log unit. The variation does not seem correlated to age, at least within the age range of the experimental group, nor to sex. In no case could any significant change in the level of the cone segment be observed. The overshooting of the cone part might vary from hardly detectable to 2 minutes. Also, the separation between the two curves over the steep part of the rod segment up to 20 minutes might be not as distinct as in figure 1. At 20 minutes and beyond the separation is, however, always clear and becomes increasingly greater, until the final level is reached. The final separation between the normal level of adaptation and the lowest level reached at termination of the experiment after exposure to ultra-violet, for all observers, is given below.

OBSERVER	AGE	SEX	MEAN SEPARATION IN LOG UNITS
T. H. C.	18	m	0.24
M. L.	19	f	0.24
E. E. F.	21	f	0.28
D. A. J.	25	f	0.24
G. A. B.	26	m	0.29
E. W.	43	m	0.23
		Mean =	0.253

The mean increase in light intensity for threshold recognition among 6 observers is 0.253 log unit. This indicates that roughly 1.8 times as much light is needed for threshold response at "complete" dark adaptation after preëxposure to light containing wave-lengths as low as 290 mμ.

Similar effects on final dark adaptation thresholds after prolonged exposure to sunlight, moderately rich in ultra-violet, have been described recently.[6] An overshooting of the cone segment and a temporary rise of final thresholds of the same order of magnitude as described here are noticed. Ultra-violet as a cause is not mentioned. It seems probable, however, according to some of our tests with preëxposure to light reflected from snow, that the changes in final level are not due to glare, but rather to the ultra-violet.

On two observers tests were made comparing the effects of light filtered by Noviol with those of light filtered by plate glass, which excludes the strong mercury lines at 297, 302 and 313 mμ, but transmits the 365 mμ band at full strength. The data are given in figure 2. Besides a difference in the onset of rod adaptation for the two observers, both show an overshooting of the cone segment for the plate glass curves of about 1

minute. The mean final threshold difference is 0.15 log unit, 0.1 log unit less than with crown glass, due to the reduction in effective ultra-violet radiation.

Comparing AO Cruxite which transmits about 20 per cent at 365 mμ with Noviol, the ensuing dark adaptation curves are practically identical. At least no final threshold differences can be noticed. There are, however, slight irregularities at the cone-rod transition which suggest overshooting

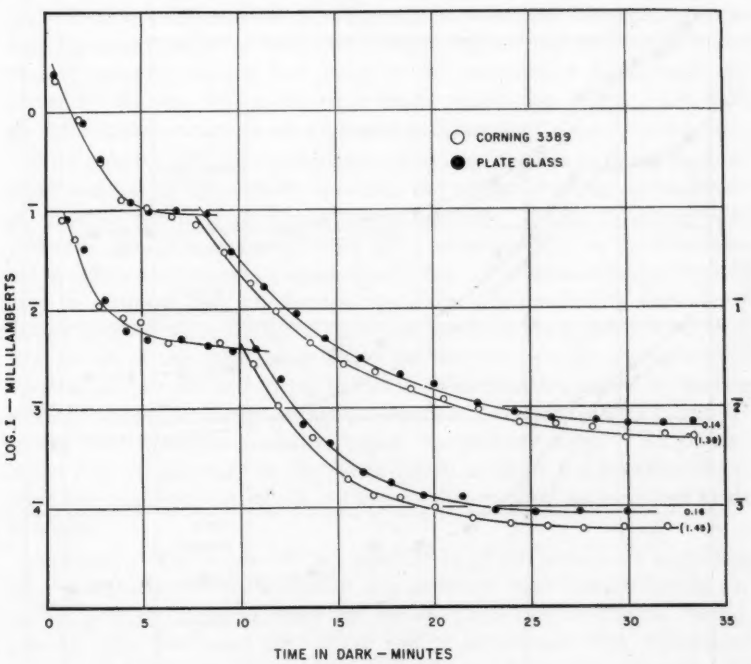

FIGURE 2

The course of dark adaptation after preëxposure to light free of ultra-violet (open circles) and light filtered by plate glass (black circles). Due to the ultra-violet, the rod adaptation begins later and the thresholds are higher.

of the Cruxite curve. Also the initial steepness of the rod segment might be less for Cruxite. From 15 minutes onward the normal and the Cruxite curves are, however, identical, indicating that any small ultra-violet effect produced by the reduced transmission at 365 mμ, recognizable at the beginning of rod adaptation, has disappeared at a time when previously the effect of exposure to ultra-violet was most pronounced.

Compared with the results on the eyes of baby chicks the effect on human dark adaptation is considerably smaller. In the chick an intensity increase by a factor of 12.5 was necessary (crown vs. Noviol) as against 1.8 for the human eye, a ratio of 6.6:1. Assuming that most of the effective ultra-violet is absorbed by the lens, one should expect a considerably

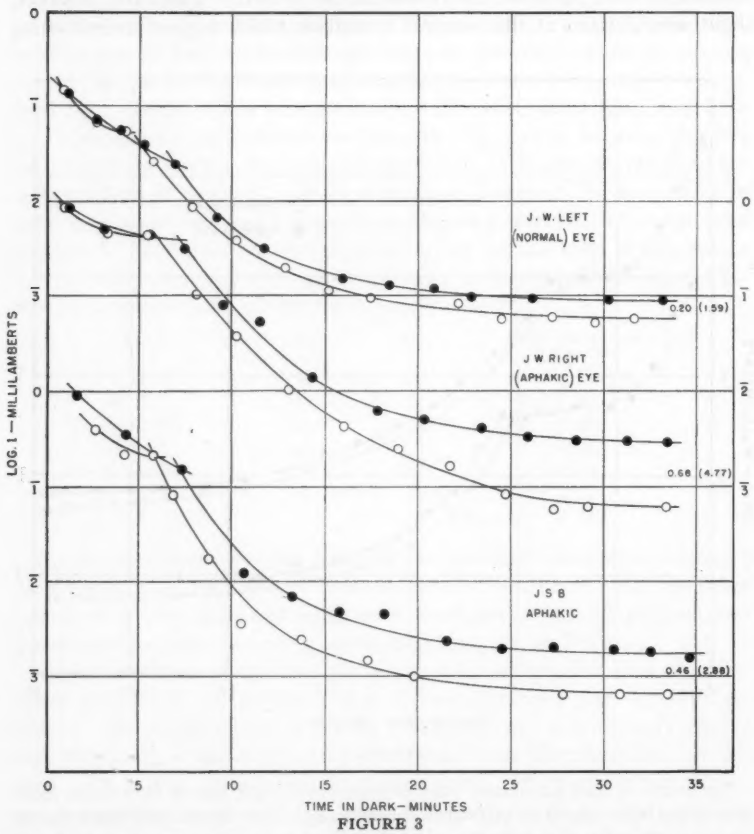

FIGURE 3

Dark adaptation in aphakics: The normal (left) eye of J. W. gives curves similar to those presented in figure 1. For the aphakic eye the separation between the normal and the ultra-violet curve is considerably increased, due to more effective action of ultra-violet upon the retina. The same conditions are found in J. S. B.

greater effect in aphakics. Two observers were available. J. W., age 26, had the lens of his right eye removed several years ago, the left eye having normal vision. His normal eye gives a final threshold separation of 0.20

log unit which is slightly below the average of the group of 6 mentioned previously. For the aphakic eye the separation between the Noviol and the crown curves becomes increasingly greater after the cone-rod transition, until a final separation of 0.68 log unit is reached, corresponding to an increase in light intensity by a factor of 4.77 for threshold recognition. In J. S. B., 30 years, both eyes are aphakic; one eye having better vision is used for test. The results are similar to those for J. W. with the exception that the final separation is only 0.46 log unit, or a factor of 2.88. Even while there is a difference of 0.22 log unit between the two aphakics, the final threshold levels for both are so much higher than previously found that it becomes evident that much of the ultra-violet is normally absorbed by the lens which otherwise would reach the retina. The data on the aphakic observers are presented in figure 3.

With only 0.1 per cent transmission at 365 mμ, there is no doubt that the small amount of ultra-violet reaching the retina produces considerable physiolgical effects in proportion to its intensity. In the human eye, as well as in the chick, the ultra-violet effect seems entirely on the rod thresholds, whereas the cones remain unaffected. For both types of eyes it may be assumed that an effect on the cones is prevented by their dense filter pigments, while the ultra-violet can act upon the pigment-free rods.[7] The action of the ultra-violet might be directly upon the photosensitive material of the rods, or it might be due to desensitization caused by fluorescence of the ocular media during preëxposure. In both cases a longer recovery time would be needed to regain maximal sensitivity. At present it can only be pointed out that ultra-violet radiation has peculiar effects upon the sensitivity thresholds of the rods, disregarding the locus and mode of action.

Summary.—The course of dark adaptation of the human eye is studied after preëxposure to the radiation of a mercury vapor lamp, filtering out the ultra-violet between 290 mμ and the visible to various extents. Exposure to light free from ultra-violet results in uniform dark adaptation curves. Addition of ultra-violet below 365 mμ affects rod adaptation by causing a later onset of rod adaptation and raising the final thresholds appreciably above the normal level. The cone adaptation is not affected. The final level reached is a function of the extent of the ultra-violet spectrum. The lens, having a high ultra-violet absorption, reduces the ultra-violet action upon the retina which can be demonstrated on aphakic eyes in which the ultra-violet action on dark adaptation is considerably increased.

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† The experiments were carried out with a visual discriminometer at the Laboratory of Industrial Physiology, Harvard School of Business Administration, which kindly was

made available for the purpose. I feel particularly indebted to Miss D. A. Jameson for her generous help in these experiments.

[1] Wolf, E., these PROCEEDINGS, **31**, 349 (1945); **31**, 236 (1945).
[2] Friedrich, W., and Schreiber, H., *Arch. ges. Physiol.*, **246**, 621, 790 (1943).
[3] Ludvigh, E., and McCarthy, E. F., *Arch Opth.*, **20**, 37 (1938).
[4] Wald, G., *Science*, **101**, 653 (1945).
[5] Crozier, W. J., and Holway, A. H., *Jour. Gen. Physiol.*, **22**, 341 (1939).
[6] Hecht, S., *The Air Surgeons Bulletin*, **2**, 45 (1945).
[7] Wald. G., and Zussman, H., *Jour. Biol. Chem.*, **122**, 449 (1938).

EXPERIMENTS ON SEXUAL ISOLATION IN DROSOPHILA. VIII. INFLUENCE OF LIGHT ON THE MATING BEHAVIOR OF DROSOPHILA SUBOBSCURA, DROSOPHILA PERSIMILIS AND DROSOPHILA PSEUDOOBSCURA

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Philip, Rendel, Spurway and Haldane[1] and Rendel[2] found that cultures of *Drosophila subobscura* Collin cannot be kept permanently in a dark room because no matings take place in this species in the absence of light. Furthermore, several mutant types with abnormal eye colors proved to be male sterile; for example, white eyed males, although they are positively phototropic like the wild type, do not respond to moving contours and produce no offspring. Rendel[2] also points out that the males of the mutant yellow (yellow body color) are discriminated against in mating by the females of some, but not all, wild type strains. Yellow females produce offspring easily when placed with wild type males. These findings are the more interesting and unexpected since Mayr and Dobzhansky[3] found that in *D. persimilis* Dobzhansky and Epling and in *D. pseudoobscura* Frolova mating and insemination occur freely in the presence or absence of light. Cultures of these species can be kept in a dark room generation after generation. Furthermore, when females of these two species are placed together with males of one of them, a significantly greater proportion of conspecific than of foreign females are inseminated and this selectivity of mating is not affected by light or by darkness. It follows that representatives of these species are able to discriminate between conspecific and foreign mates in the absence of light.

D. subobscura, *D. persimilis* and *D. pseudoobscura* are three morphologically very similar species; yet their mating reactions are profoundly different with respect to at least one environmental agent, namely, light. Such variations in the mating reactions in related species may be very important biologically if they lead to sexual isolation between the species. It might be interesting to resolve some representative examples of sexual isolation into their component parts and to identify the variables which enter into a sexual isolation. Such differences in the behavior of related species as the dependence or independence of mating on presence or absence of light lend themselves readily to quantitative and qualitative study. The results of an exploratory study of this type is reported in the present paper.

We wish to express our sincere appreciation of the courtesy of Professor J. B. S. Haldane who let us have a strain of *D. subobscura* collected in England and bred in his laboratory. Professor H. J. Muller very kindly transported this strain to this country. Professor S. Hecht and Drs. S. Shlaer and Ch. Hendley of the Laboratory of Biophysics, Columbia University, have very kindly helped to arrange the experiments on light intensities. To Mr. George Streisinger we are obliged for his assistance with the experiments at the beginning of the investigation.

Material and Methods.—A single strain of each of the three species has been used in all the experiments to be described: the English strain of *D. subobscura*, *D. persimilis* from Stony Creek, California, and the orange mutant strain of *D. pseudoobscura*. Adults of *D. subobscura* were transferred without etherization to fresh culture bottles at intervals of from one to several days and kept in a well-lighted laboratory room at 22°–24°C. The bottles with eggs deposited in them were placed in a dark constant temperature room at 19°C. Cultures of *D. persimilis* and *D. pseudoobscura* were treated similarly except that they were allowed to develop at room temperature.

Effects of Light and Darkness on the Frequency of Insemination.—The experiments consisted of placing 10 to 15 females of one species with a similar number of males of the same or of a different species in 1 × 3¼-inch glass vials with food and examining the females for the presence of sperm after a certain number of days. At the beginning of each experiment the flies were not more than 24 hours old after hatching from the pupae. Some of the vials (light series) were placed on a shelf in the laboratory out of the direct sunlight but exposed to the diffuse light of the room. Other vials (dark series) were individually wrapped in heavy black paper and placed in an opaque cardboard box which was then put on the shelf with the vials of the light series. After a desired number of days, all females were dissected and their seminal receptacles were examined under a microscope for sperm.[3] The data obtained in the parallel experiments of the light and dark series are summarized in table 1.

TABLE 1

NUMBER OF FEMALES DISSECTED (n) AND PER CENT FERTILIZED (%) AFTER SEVERAL DAYS' EXPOSURE IN LIGHT AND IN DARKNESS

CROSS	LIGHT			DARK		
	DAYS	n	%	DAYS	n	%
subobscura ♀ × subobscura ♂	3–4	60	80.0	5–9	72	0.0
persimilis ♀ × persimilis ♂	3–5	41	75.6	9	22	100.0
subobscura ♀ × persimilis ♂	7–14	118	8.5	7–9	136	2.9
persimilis ♀ × subobscura ♂	7–13	80	15.0	7–12	80	1.3*
subobscura ♀ × pseudoobscura ♂	9–11	64	21.9	8–15	152	7.2
pseudoobscura ♀ × subobscura ♂	9–13	96	25.0	10–15	128	0.0

* A single female found to contain sperm in this cross is probably due to an experimental error.

It can be seen that none of the 72 *D. subobscura* females were inseminated by males of their own species after as long as 5–9 days together in darkness. By contrast, about 80% of the females were inseminated after 3–4 days in the light. The behavior of *D. persimilis* is quite different since males of this species, as well as of *D. pseudoobscura*, inseminate females of their respective species equally as rapidly in light as in the dark (for more data on the latter species see Mayr and Dobzhansky[3]).

Hybrids of *D. persimilis* and *D. pseudoobscura* can be obtained in the laboratory rather easily. The viability of these F_1 hybrids is not inferior to that of the parents. Crosses of *D. subobscura* with *D. persimilis* or with *D. pseudoobscura* never produced viable hybrids, larvae or adults, in our experiments. Nevertheless, as shown in table 1, cross-insemination between these species does occur although much less frequently than matings within a species. In the light, *D. subobscura* males have inseminated as many as 25% of *D. pseudoobscura* and 15% of *D. persimilis* females in 7–13 days. No inseminations by *D. subobscura* males have been observed in the dark series. (One female of *D. persimilis*, among 80 females exposed for 7–12 days to *D. subobscura* males, contained sperm, cf. table 1, but this is almost certainly an experimental error.)

Although *D. subobscura* females and males do not mate in the dark, an appreciable number of inseminations have been observed in the crosses that involve *D. subobscura* females and *D. persimilis* or *D. pseudoobscura* males. These interspecific matings have been observed both in the light and in the dark series but, interestingly enough, they are relatively more frequent in the light than in the dark. Light is essential for normal sexual activity of *D. subobscura* males. *D. subobscura* females accept some courting males in the dark although they do so less frequently than in the light. Light is not an essential factor for mating of either males or females of *D. persimilis* or of *D. pseudoobscura*.

The following experiment was intended to clarify the role of the light in the mating behavior of *D. subobscura*. Several vials each containing 10

males and 10 females of *D. subobscura* were prepared. These vials were placed in a small opaque box which was, in turn, placed in a larger box. The vials and boxes were kept in a drawer of a desk. Several times each day for 8–10 days, these vials were exposed to the light of the room (several times to direct sunlight) until the first courtship was observed in any of the vials; the vials were then quickly shaken, covered and replaced in the desk. After 8 days, 15 females were dissected and after 10 days, 18 more. None of these females had been inseminated. Apparently darkness prevents the completion of matings which have proceeded to the courtship stage. There seems to be no appreciable carrying over of sexual activity from periods of light exposure into darkness.

In order to test the rapidity of matings of *D. pseudoobscura* in the dark, vials with food containing 10 males and 10 females were prepared and placed within the series of boxes mentioned above. Females were dissected at the end of 1, 2, 4 and 7 hours. All of the females were inseminated in those vials which were left for 2 hours or more; 7 females in the vial left for 1 hour contained sperm. Another series of vials was prepared without food and placed in the dark for times ranging from 15 to 90 minutes (15-minute intervals). The number of inseminated females varied from 8 after 30 and 45 minutes of exposure to 4 after 1 hour. Exposure for 1 $^1/_2$ hours and 15 minutes gave identical results—7 females inseminated. Activity in the dark, then, begins at once and proceeds at a pace comparable to that to be described in the next experiment.

Direct Observations on the Sexual Behavior.—Females and males of all three species were aged for 1–2 weeks in isolation in a dark room at 19°C. Clean vials without food were placed on vial racks covered with white paper; 2 females of one species and 2 males of the same or of a different species were introduced, without etherization, into each vial. The behavior of the flies in the vials were then observed for two hours under normal daylight conditions on a table before a window (direct sunlight being avoided). Ordinarily 20 vials were under observation at one time; 5 vials of each of the four possible combinations A♂ × A♀, A♂ × B♀, B♂ × A♀, B♂ × B♀, where A is *D. subobscura* and B is *D. pseudoobscura* or *D. persimilis*. At times it was expedient to increase the number of vials of a certain cross at the expense of other crosses, but never more than 20 vials were used simultaneously since this was found to be the maximum number that could be handled efficiently.

Three stages can be distinguished in the mating of Drosophila: courtship, copulation and insemination. The occurence or non-occurrence of the last of these stages, insemination, can be determined with certainty by dissection of the female and microscopic examination of her sperm receptacles and vagina. It is slightly more difficult to decide whether copulation has or has not taken place. As a rule, absence of space between the tips of the

abdomens of the flies involved and difficulty of the female in dislodging the male were taken as evidence that copulation had occurred. The occurrence of courtship is the most difficult to ascertain and much depends upon an individual observer. Detailed descriptions of the courtships of *D. subobscura* has been given by Rendel[2] and of *D. persimilis* and *D. pseudoobscura* by Mayr.[4] These descriptions have been confirmed by us. The courtships involve males sparring with females, wing flicking, wing extension and vibration, and finally circling and mounting. All three species indulge in sparring, i.e., exchanging of taps with the forelegs. *D. subobscura* males flick their wings while males of the other two species do not. Wing extension in *D. persimilis* and *D. pseudoobscura* consists of extending one wing parallel to the female's body, usually anteriorly, while the male stands facing the female from either side. In *D. subobscura* wing extension occurs while the male stands in front of and facing the female and consists of extending both wings at right angles to the male's body.

Males often court other males but such courtships were not included in the data. Since courtships are not always continued after sparring and since sparring is of short duration and liable to be overlooked, sparring alone was not counted as courtship. *D. subobscura* males often indulge in wing flicking on occasions other than courtships, hence flicking was not considered to constitute a courtship unless the male did it insistently before a female. Extending and vibrating a wing(s) was taken in all cases to be a bona fide courtship. If a courting pair separated and there was no attempt on the part of the male to continue the courtship, that courtship was regarded completed. If, after a lapse of time, the same male resumed courting, this fact was recorded as a separate courtship. However, if the male followed a female and his behavior seemed to indicate a continuing interest in her, his entire performance was considered a single courtship. The total results of the two-hour observational periods are given in table 2. Table 3 shows some of the data reported in table 2 recalculated for a single female for the four consecutive half-hour periods of observation.

TABLE 2

NUMBER OF COURTSHIPS, COPULATIONS AND INSEMINATIONS DURING TWO-HOUR EXPOSURE PERIODS OF AGED FLIES UNDER NORMAL DAYLIGHT CONDITIONS

CROSS	FEMALES EXPOSED	COURTSHIPS TOTAL	COURTSHIPS PER ♀	COPULATIONS TOTAL	COPULATIONS PER ♀	INSEMINATIONS TOTAL	INSEMINATIONS PER ♀
subobscura ♀ × subobscura ♂	86	118	1.37	17	0.20	..	..
persimilis ♀ × persimilis ♂	60	61	1.02	32	0.53	..	..
pseudoobscura ♀ × pseudoobscura ♂	66	104	1.58	40	0.61	..	..
subobscura ♀ × persimilis ♂	60	52	0.87	0	0	0	0
persimilis ♀ × subobscura ♂	60	186	3.10	50	0.83	6	0.10
subobscura ♀ × pseudoobscura ♂	70	81	1.16	0	0	0	0
pseudoobscura ♀ × subobscura ♂	68	88	1.29	5	0.07	0	0

TABLE 3

COURTSHIPS (CRT) AND COPULATIONS (COP) PER FEMALE BY HALF-HOUR INTERVALS OF EXPOSURE

CROSS		1ST	2ND	3RD	4TH	TOTAL	FEMALES EXPOSED
subobscura ♀ × subobscura ♂	Crt	0.45	0.23	0.13	0.18	0.98	56
	Cop	0.07	0.02	0.02	0.02	0.13	
persimilis ♀ × persimilis ♂	Crt	0.67	0.37	0.10	0.03	1.17	30
	Cop	0.53	0.30	0.07	0	0.90	
pseudoobscura ♀ × pseudoobscura ♂	Crt	0.59	0.47	0.32	0.20	1.58	66
	Cop	0.30	0.14	0.11	0.06	0.61	
subobscura ♀ × persimilis ♂	Crt	0.17	0.13	0.30	0.07	0.67	30
	Cop	0	0	0	0	0	
persimilis ♀ × subobscura ♂	Crt	1.73	0.73	0.60	0.33	3.40	30
	Cop	0.60	0.20	0.07	0.07	0.93	
subobscura ♀ × pseudoobscura ♂	Crt	0.27	0.26	0.34	0.29	1.16	70
	Cop	0	0	0	0	0	
pseudoobscura ♀ × subobscura ♂	Crt	0.37	0.40	0.24	0.29	1.29	68
	Cop	0.03	0.04	0	0	0.07	

An inspection of table 2 reveals facts that could not have been predicted on the basis of the data presented in table 1, which shows interspecific inseminations to be much less frequent than intraspecific ones. Table 2 shows that the number of courtships per female is of the same order of magnitude in all crosses. In fact, the greatest number of courtships per female occur when *D. subobscura* males are placed with *D. persimilis* females and the smallest number in the reciprocal cross. Table 3 indicates, however, that this uniformity is arrived at differently in the interspecific and intraspecific crosses. When the females and males belong to the same species, the number of courtships declines rapidly in the consecutive half-hour periods. When the females and males belong to different species, the frequency of courtships remains more nearly constant throughout the two hour period. The most probable explanation of these relationships lies in that a much higher proportion of intraspecific than of interspecific courtships result in copulations. (See below.) Consequently, the courtship behavior subsides more rapidly in the vials containing conspecific females and males than in vials containing representatives of different species.

During the first half hour of observation, when few of the individuals had copulated previously, a high proportion of the courtships between males and females of the same species are followed by copulations. Data in table 3 show that the ratio copulations/courtships is highest in *D. persimilis*, intermediate in *D. pseudoobscura* and lowest in *D. subobscura*. Behavior within the three species is similar: genitalia are brought into contact, the male mounts and the pair remains quiet from 3 to 10 minutes (average $6^1/_2$ minutes) after which separation occurs. Whenever dissected the females

contained spermatozoa. In the combinations of *D. subobscura* females with *D. persimilis* or *D. pseudoobscura* males (tables 2 and 3), no normal copulations at all have been observed although they must take place as inseminations have been recorded for these crosses (table 1). The female runs away from the courting male, repulses him by extending her middle leg toward him, rotates her abdomen, or else the male breaks off the courtship without attempting to mount. If he mounts, as he frequently does, the pair separate immediately. The situation, therefore, is analogous to that found by Mayr[4] in the crosses of *D. persimilis* and *D. pseudoobscura*. The precise nature of the difficulty which prevents the copulation from being successful is not clear. It may be noted that the external genitalia are morphologically identical in *D. persimilis* and *D. pseudoobscura*, while those of *D. subobscura* males differ in several characters both of the genital arch, the anal tubercle and the penis apparatus.

When *D. subobscura* males and *D. pseudoobscura* or *D. persimilis* females, expecially the latter, are involved, things go differently. The male mounts and copulation seems to be successful but in a few seconds the female begins to struggle in violent efforts to free herself from the male. The pair frequently falls on the bottom of the vial, the male attempting to maintain his position and the female striving to dislodge him with kicks by her hind legs. The female succeeds in freeing herself in from a few seconds to about two minutes after the start of the struggle; less than 30 seconds is required in the majority of cases.

Only 6 out of the 50 *D. persimilis* females and none of the *D. pseudoobscura* females which have copulated with *D. subobscura* males contained any spermatozoa on dissection. This means that a majority of the interspecific copulations do not result in sperm delivery. It can be surmised that insemination occurs only in those cases when copulation lasts longer than the average.

Intensity of Illumination and Sexual Activity of D. subobscura.—The courtships and copulations of *D. subobscura* males and females were observed by placing vials each containing 2 females and 2 males at various distances (1–5 meters) from a 150-watt Reflectorflood bulb in a dark room at the Department of Biophysics of Columbia Univesity. Observations were made by walking from vial rack to vial rack. Each experiment lasted for two hours. Ordinarily two vials were placed at each position. Inasmuch as a courtship is of such short duration that it can begin and end in the time it takes an observer to make a circuit of all vials (± 1 min.) while a copulation lasts for several minutes, the ratios copulations/courtships in the present data are not comparable to those obtained from the above data. Table 4 summarizes the results of these observations.

TABLE 4

COURTSHIPS AND COPULATIONS IN *D. subobscura* AT DIFFERENT LIGHT INTENSITIES (FOOT-CANDLES)

LIGHT INTENSITY	TOTAL FEMALES	COURTSHIPS		COPULATIONS	
		TOTAL	PER ♀	TOTAL	PER ♀
85.4	22	8	0.36	2	0.09
27.0	22	59	2.68	8	0.36
10.3	22	29	1.32	1	0.05
4.5	22	7	0.32	2	0.09
2.5	20	14	0.70	1	0.05

Table 4 shows that both very bright and dim light are unfavorable for sexual activity. The flies were most active when placed in light of 27 foot-candle intensity. Sexual activity seems to be correlated in this case with mobility of the flies because in the vials in which many courtships were taking place, the flies were moving about to a greater extent than in the others. The latter point is borne out in that flies placed behind a black screen in the same dark room and observed by light reflected from a white card were very quiet, moved very slowly if at all, and never sparred, courted or copulated. It must be admitted, however, that it is difficult to observe the behavior of flies accurately in light of less than 2.5 foot-candles intensity.

Behavior of D. subobscura in Red Light.—Bertholf[5] has shown that wild type *D. melanogaster* flies are relatively insensitive to red light and that the upper limit of sensitivity lies at 650–675 μ wave-length. Observations on the behavior of the flies in red light, therefore, should give an approximate idea about their behavior in the absence of light. A glass filter transmitting light of 600–610 μ was placed in the lamp used in the previous experiments. Energy and intensity measurements were not made; intensity of red light in foot-candles is meaningless and energy is unimportant inasmuch as a point of non-activity rather than a threshold was what was desired.

When the two vials each containing two pairs of D. *subobscura* were placed at the distances from the light source mentioned above, no sexual activity of any type was observed. The flies remained quiet or moved slowly in the vial. There was no orientation of the flies with respect to the light.

When the flies used were *D. pseudoobscura*, courtships and copulations proceeded as they do in the light. Although, in general, there was no change in behavior, male flies were observed on two occasions extending and vibrating their wings towards the posterior end of the females and attempting to mount the anterior end.

Since the absence of activity in *D. subobscura* and the presence of activity in *D. pseudoobscura* in red light resemble the situation existing in the absence of light, vials containing five females of one species and five males of the same or the other species were prepared and observed for two hours.

There was no indication of courtships on the part of *D. subobscura* males either with their own or with *D. pseudoobscura* females. *D. pseudoobscura* males courted and copulated with their own females and courted *D. subobscura* females. As in the observations recorded in table 2, no copulations of *D. pseudoobscura* males with *D. subobscura* females were seen; each courtship was terminated when the female moved away or rotated her abdomen.

Summary.—Mating takes place with or without light in *Drosophila persimilis* and *D. pseudoobscura*, while *D. subobscura* mates only in the presence of light. Males of *D. persimilis* and *D. pseudoobscura* inseminate some *D. subobscura* females, the frequency of this cross-insemination being greater in the light than in the dark. *D. subobscura* males inseminate some females of the other two species in the light but not in the dark. Light intensity of the order of 30 foot-candles was found to be close to the optimum for mating in *D. subobscura*, but no mating and no courtship take place in this species in red light of an intensity which permits observation. Direct observations disclose that, in the light, males of any one of the three species court about equally frequently females of their own and of the other two species. However, interspecific copulation occurs only seldom, and if it does the female dislodges the male in usually less than 30 seconds, ordinarily before sperm ejaculation takes place.

[1] Philip, U., Rendel, J. M., Spurway, H., and Haldane, J. B. S., *Nature*, **154**, 260–262 (1944).

[2] Rendel, J. M., *Jour. Genetics*, **46**, 287–302 (1945).

[3] Mayr, E., and Dobzhansky, Th., these PROCEEDINGS, **31**, 75–82 (1945).

[4] Mayr, E., *Ibid.*, **32**, 128–137 (1946).

[5] Bertholf, L. M., *Zeits. vergl. Physiol.*, **18**, 32–64 (1932).